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Recovery of tree species functional composition in eucalypt plantations with natural regeneration differs among canopy strata

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ABSTRACT

Tree monocultures have been promoted globally to supply timber; yet, a high diversity of native trees can establish in less intensively managed plantations, allowing to both harvest timber and transition towards a more natural forest. However, little is known about the functional recovery of native trees under plantations, which is critical for biodiversity conservation and ecosystem services. Here, we evaluate how functional composition of tree strata differs between two restoration methods (eucalypt plantations with natural regeneration and naturally regenerating forests) and how this is affected by stand age, climatic water deficit, and soil characteristics. We established 129 plots in two restoration methods and mature forest as reference, in São Paulo state, Brazil. We divided tree stratum in each plot into different canopy strata using perfect plasticity approximation. We measured five key traits that are important for fire resistance (bark thickness), drought tolerance (wood density), productivity (specific leaf area and leaf thickness), and nutrient cycling (nitrogen-fixing ability) for 393 species and calculated for each stratum community-weighted mean trait values. Community traits were mostly affected by canopy strata, the interaction between canopy strata and restoration method, and water availability. Eucalypt trees dominated the upper strata of plantations, presenting higher wood density, tougher leaves, and thicker bark, reflecting the drought and fire adaptation of eucalypts. The lower strata of eucalypt plantations and naturally regenerating forests had similar functional composition. Our results suggest that eucalypt plantations can be used as a tool to facilitate natural regeneration and restore ecosystem functioning in degraded areas.

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1. Introduction

Forest landscape restoration initiatives have been encouraged globally and locally to mitigate the negative consequences of forest loss on climate change, as well as to conserve biodiversity and provide ecosystem services, including timber production. These initiatives are composed by, among others, the Bonn Challenge on a global scale, the Initiative 20 × 20 in Latin America and the Caribbean, the AFR100 in Africa, and the United Nations 2021–2030 “Decade on Ecosystem Restoration” worldwide. All these initiatives have catalyzed local projects that target different outcomes as priorities and employ different restoration methods in various socio-ecological conditions. Understanding the pros and cons of different methods for different types of outcomes is then a critical research gap for supporting decision-making and reforestation best practices.

Restoration approaches vary largely in terms of the level of interventions required to reestablish tree cover, covering a gradient ranging from the spontaneous recolonization of regenerating trees to tree planting in the entire area (Chazdon et al., 2021). Natural regeneration, also known as passive restoration, is the more cost-effective approach for carbon and biodiversity recovery across large scales, but can be applied only on particular biophysical conditions, where landscape resilience is high and previous land use intensity is low (Chazdon and Guariguata, 2016; Poorter et al., 2021a). Alternatively, tree planting is employed when site regeneration capacity is low and/or there are commercial interests in producing timber or non-timber forest products from planted trees (Poorter et al., 2021b). When trees are planted for commercial reasons, monocultures are the prevailing approach, as they maximize the production of targeted products and can be implemented and managed with high operational efficiency. In fact, most reforestation initiatives worldwide are plantations of utilitarian tree species, for timber, food, and other uses (Martin et al., 2021; Schubert et al., 2024). Although well-established to generate tree-based products, there has been an intensive debate on the role of tree monocultures as a means of restoration or to provide a wide range of ecosystem services (Lewis et al., 2019).

Industrial, large-scale tree monoculture plantations, that are sometimes referred to as “green deserts” (Acosta, 2011), are usually characterized by even-aged, structurally uniform tree stands lacking naturally regenerating tree species in the understory, due to intensive plantation understory cleaning. Some studies indicate, however, that this is not always the case (Lugo, 1997; Bremer and Farley, 2010; Lemenih, Bongers, 2010; Simões et al., 2024), as monoculture plantations can create favorable microclimate conditions that facilitate understory recolonization by native species, while also contributing to soil protection, carbon stocks, and timber production when less intensively managed or unmanaged (Brockerhoff et al., 2008, 2013; Cesar et al., 2018; Simões et al., 2024). Classical studies have even shown that some commercial trees could be used as nurse plants to kickstart natural regeneration in degraded lands (Guariguata et al., 1995; Lugo, 1997; Ashton et al., 1998). Although there is enough evidence about the potential use of some commercial trees as a transition stage towards long-term forest restoration, and of the use of the revenues from timber production to offset restoration costs (Amazonas et al., 2018; Brancalion et al., 2020), little is known about the long-term ecological dynamics of native species regeneration growing underneath commercial monoculture stands, especially about their functional properties.

The recovery of community functional properties is important for the recovery of ecosystem functions and stability of restored forests (Cadotte et al., 2011; Carlucci et al., 2020). Functional properties are closely linked with functional traits, which are characteristics of an organism that are relevant to its response to the environment and/or to its effect on the ecosystem functioning (Violle et al., 2007; Díaz et al., 2013). Consequently, the value and range of functional traits of the organisms present in a given ecosystem, i.e., functional diversity, can be used as a proxy for ecosystem functioning (Díaz and Cabido, 2001; Hooper et al.,

2005). A critical component of functional diversity is functional composition, which represents the average trait value of plants in the community. By assessing the functional composition of restored forests, it is possible to understand the successional mechanisms these forests undergo over time (Poorter et al., 2021b). Previous studies have shown that succession is modulated by water availability in areas with pronounced dry season, while it is driven by light availability in areas where rainfall is not a limiting factor (Lohbeck et al., 2013; Letcher et al., 2015; Poorter et al., 2019b, 2021b).

As forest succession proceeds, the environmental conditions change and, as expected, functional composition and diversity vary. Long-term successional changes in functional composition over time have been studied primarily through chronosequences, as monitoring succession in the same site across time is more challenging, and has been done only for a few tropical forest sites (Norden et al., 2015). A complementary approach is to evaluate how the ecological characteristics of the regenerating community change over the vertical strata, which can be used as a proxy of the different fluxes of recruitment that a given forest stand experienced over time. Height-structured competition for light in the stratum composed by trees, which results in multiple canopy strata, is a vital process determining forest dynamics (Purves et al., 2008; Matsuo et al., 2024a), since it allows to account for differences in tree size, forest successional stages, and light availability (Rüger et al., 2023). At the beginning of succession, shade-intolerant species colonize the area, and as succession proceeds, there is a shift in dominance towards shade-tolerant species (Chazdon, 2014). While light-demanding canopy species have functional traits associated with resource acquisition and growth, shade-tolerant understory species have functional traits related to resource conservation and persistence in wet regions. In dry regions, early successional conditions are hot and dry, colonizing species show conservative strategies. When succession proceeds and the vegetation builds up, the microclimate conditions become cooler, more humid, and benign, which facilitates the establishment of more acquisitive, later-successional species (Lohbeck et al., 2013; Poorter et al., 2019b).

Currently, functional restoration studies are mainly focused on temperate ecosystems (Carlucci et al., 2020), on multi-species plantations (Aubin et al., 2009; Audino et al., 2014; Ilunga et al., 2015), or on few ecosystem functions (e.g., seed dispersal (Evaristo et al., 2011; Harikrishnan et al., 2012; Cesar et al., 2018), but see Brouwer et al., 2025). Considering that tree monoculture plantations are widespread across the globe and are increasingly used in forest landscape restoration initiatives, it is essential to understand if and under which conditions these plantations can contribute to the recovery of ecosystem functioning.

In this study, we address two research questions. First, we evaluate if functional composition varies with restoration type by comparing *Eucalyptus* L'Hér. and *Corymbia* K.D.Hill & L.A.S.Johnson (hereafter eucalypt) plantations with natural regeneration with naturally regenerating secondary forests (hereafter naturally regenerating forests). Second, we assess how 1) stand age, 2) canopy strata, 3) climatic water deficit and 4) soil characteristics affect the functional composition of these two restoration methods. We hypothesized that in eucalypt plantations with natural regeneration, the understory would be more shaded and consist of species with more conservative trait values than in naturally regenerating forests; and that: 1) during succession, there would be a change from acquisitive trait values of pioneers towards conservative trait values of later successional species in both restoration methods; 2) each canopy strata would differ in their trait values from other canopy strata because they are dominated by species that attain different maximum sizes and differ in their trait characteristics (light-demanding canopy species have acquisitive trait values, sub-canopy species have intermediate trait values and shade-tolerant understory species have conservative trait values); 3) in dry forests, leaf trait values would be more acquisitive because some species are deciduous and have short-lived leaves and stem traits would be conservative to avoid

drought-induced cavitation and stem damage; 4) soil characteristics related to high nutrient and water availability would result in acquisitive traits. To our knowledge, this is the first study to integrate a functional trait approach with stratified sorting of trees across multiple canopy strata to understand the potential contribution of eucalypt plantations with regeneration to the recovery of ecosystem functioning.

2. Material and methods

2.1. Study areas

We carried out the research along a climatic gradient in the state of São Paulo, Brazil (Fig. 1). The state of São Paulo is located in the Southeast region of Brazil, and it is the most densely populated state in the country. The largest ecoregion of the state is the Atlantic Forest, considered a global biodiversity hotspot and a priority ecoregion for both conservation and restoration (Myers et al., 2000; Brancalion et al., 2019; Strassburg et al., 2020). The other ecoregion is Cerrado, the most biodiverse savanna in the world and also a biodiversity hotspot for conservation.

We considered two restoration methods: 1) eucalypt plantations with natural regeneration, that are, former commercial plantations where management practices - such as weeding and understory cleaning - have been discontinued or applied less intensively due to legal limitations, unsuitability to mechanization, or to promote biodiversity and enhance ecosystem services; 2) naturally regenerating forests with different ages. Additionally, we included mature forest within the studied sites, used as reference but not included in the analyses. The forest plots were distributed along five different climate types according to Köppen classification, being Cwa (humid subtropical, with dry winter and hot summer), Cfa (humid subtropical, oceanic climate, without dry season, with hot summer), Cwb (humid subtropical, with dry winter and temperate summer), Cfb (humid subtropical, oceanic climate, without dry season, with temperate summer) and Aw (tropical with dry winter)

(Alvares et al., 2013). The sampled sites, local regions (e.g., farms) comprising a set of plots, presented medium to clayey or very clayey soil textures (IBGE, 2006) (more information on sampled sites in the Suppl. Mat. S1).

2.2. Data collection

From a set of plots established in different sites in the state of São Paulo, we selected plots in sites where the two studied restoration methods and reference mature forests were present, yielding a total of 129 plots: 29 plots established in eucalypt plantations with natural regeneration, 64 plots in naturally regenerating forests, and 36 plots in mature forests. The plots were located in different local and climatic conditions (Suppl. Mat. S1: Table S1-1, Table S1-2). Naturally regenerating forests were growing on abandoned pastures ($n = 20$) and agricultural fields ($n = 1$); in areas formerly used for eucalypt ($n = 10$) or pine tree ($n = 1$) plantations, where the planted species was not present anymore after harvesting; or in a clearcut native forest for charcoal production ($n = 1$). We did not find detailed information on previous land use for 31 naturally regenerating forest plots.

Within each 900 m² plot, we collected a composite soil sample (three collection points per plot, 0–10 cm depth) to determine soil pH, sum of bases (SB), and clay percentage. Furthermore, all individual trees, shrubs, palm trees and tree ferns ≥ 5 cm in diameter at 1.3 m in height (DBH) had their diameter and total height measured and reproductive and/or vegetative branch material collected for identification at the highest taxonomic level possible, with vouchers deposited at the ESA herbarium.

Species that collectively made up 80 % of the cumulative plot basal area, and represent therefore the majority in the community (Garnier et al., 2004; Pakeman and Queded, 2007), were selected for trait measurements, resulting in 381 species. Three adult individuals (DBH > 5 cm) per species were selected for trait measurements. All traits were measured following a protocol adapted from Perez-Harguindeguy et al.,

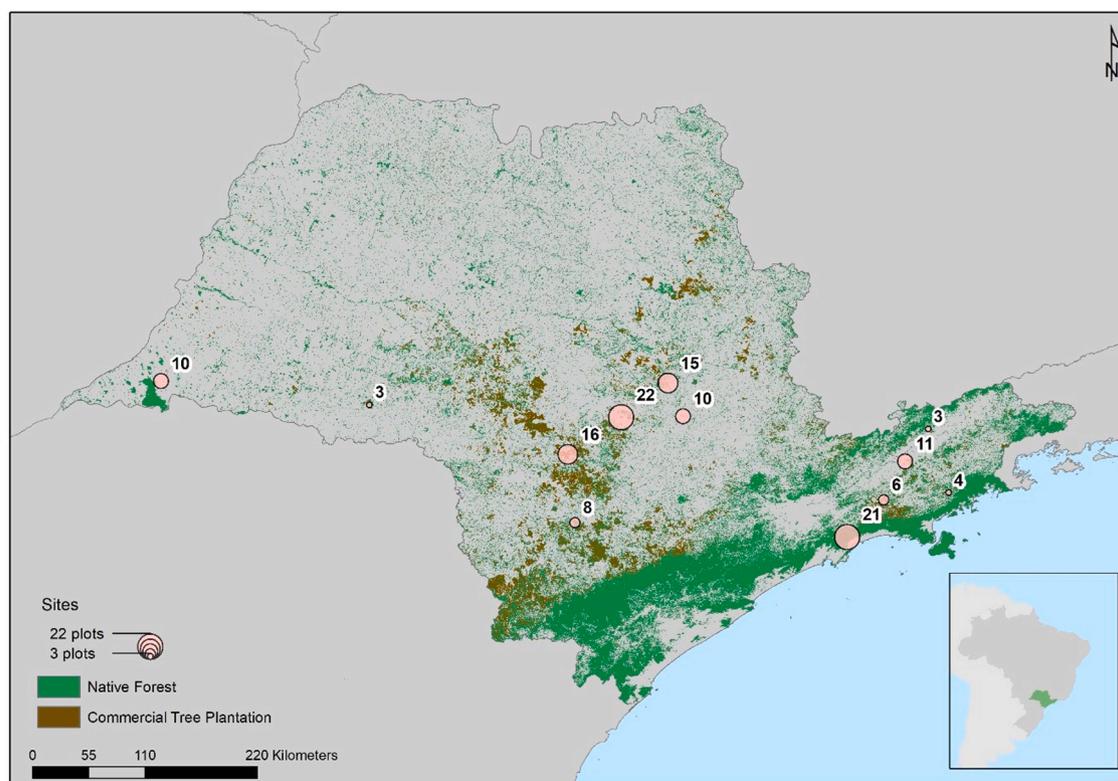


Fig. 1. Location of the study sites in the state of São Paulo, southeastern Brazil. The size of each circle is proportional to the plot count in a given site, indicated by the number by their side.

(2013). Two branches of at least 60 cm per individual with at least 10 fully developed, partially sun-lit leaves were collected. From the leaves collected in the field, two leaves or leaflets (in case of composite leaves) per individual were selected for measuring specific leaf area (SLA, m^2/kg) and leaf thickness (mm). Primary rachis and/or petioles were excluded from all leaves. Additionally, we took one wood core per tree with a 5 mm diameter increment borer from the outer bark up to the center, aiming at reaching the pith. We used the samples to calculate wood density (g/cm^3) by measuring the fresh volume (water displacement method) and dry weight of the core sample. Bark thickness (mm), that is, the thickness of the part of the stem that is external to the xylem, was measured with a bark gauge at three random points at breast height (1.3 m height).

N-fixing ability information was obtained from TRY (Kattge et al., 2011), NodDB (Tedersoo et al., 2018), and TreeCo databases (Lima et al., 2015, 2020). We included N-fixing ability as a binary variable (1 = N-fixer, 0 = not N-fixer). In case trait values were not known and could not be obtained through literature and database research (35 % of species), then average trait values from the same genus were used if available. The species without trait values were excluded from the analysis (0.18 %).

2.3. Canopy strata assignment

To analyze how older and younger trees differ in their traits, we compared the functional composition amongst different canopy strata. Trees were assigned to canopy strata using the perfect plasticity approximation, adapted from Rüger et al. (2023) and Purves et al. (2008), which assumes that trees fill up all available canopy space with their crowns when competing for light. First, we used the Tallo database (Jucker et al., 2022) to create linear models that allowed us to estimate crown radius based on tree DBH (Suppl. Mat. S2), for both native species and eucalypt trees. We filtered the Tallo database to only include angiosperms in the tropical region of South America, creating the model for native species. Then, we also filtered the Tallo database to include only eucalypts in the tropical region, and based on those data we created a specific model for eucalypt trees. With these models, we calculated the crown radius and then the crown area of each tree, assuming that the crown is a perfect circle. Then, all the trees in a given plot were ordered in decreasing order of total height as measured in the field with a hypsometer. Then, from the tallest to the shortest tree, we summed the crown area until the total area was equal to the plot area (900 m^2), composing the top stratum. The next stratum consisted of trees with a cumulative crown area larger than 900 m^2 and smaller than 1800 m^2 . This procedure was repeated until all trees in the inventory were assigned to a canopy stratum (Fig. 2-a). The fifth stratum was excluded from the analyses because only one plot had it.

2.4. Landscape and climatic variables and plot age

The functional composition of the tree communities was related to climatic water deficit, the landscape context, and stand age. The Climatic water deficit (CWD, in mm/year) is calculated as dry season precipitation minus evapotranspiration, and it was retrieved from TerraClimate (Abatzoglou et al., 2018) using the plot coordinates. CWD values ranged from 2.25 to 35.59 mm in our plots (Suppl. Mat. S1: Table S1-2). We determined the stand age by combining interviews with managers and estimations using the plot coordinates, satellite images time series, and npphen package (Chávez et al., 2023) in R software (R Core Team, 2024), which detects disturbances (including logging) through the NDMI vegetation index (Normalized Difference Moisture Index). For plantations with natural regeneration, the age was estimated as the moment when management practices were discontinued. Stand age ranged from 5 to 76 years across plots (Suppl. Mat. S1: Table S1-1, Figs. S1–1). Terrain slope the landscape metric, was determined at plot level with $30 \times 30 \text{ m}$ resolution Shuttle Radar Topography Mission

(SRTM) plugin from QGIS (Farr and Kobrick, 2000), and ranged from 0 % to 25.5 % (Suppl. Mat. S1: Table S1-2).

2.5. Data analysis

We calculated the community-weighted trait means (CWM) for each functional trait for each canopy stratum in the plot, that is, the mean of trait values in the community, weighted by the relative basal area or density of the species. To better illustrate the differences in the canopy strata among restoration methods and the reference forest, we carried out a factorial ANOVA test (two restoration methods and reference, four canopy strata) and a *post hoc* Tukey test to assess the difference in species richness (species per plot) among strata. We created Linear Mixed Models to test the effects of stand age, canopy strata, restoration method, climatic water deficit, soil characteristics (pH, sum of bases, and clay percentage), and terrain slope on the CWM values of SLA, leaf thickness, wood density, bark thickness, and N-fixing. Mature forests values are shown in the graphs as a reference but they were not included in the LMM analyses. Since we have more than one measurement per plot (i.e., four canopy strata), plot id was included in the model as a random effect. We tested including sites within the state of São Paulo as random effect, but it didn't contribute to model fitness. We excluded existent outliers and, when necessary, we transformed the variables using natural logarithm (stand age, leaf thickness, bark thickness, and proportion of N-fixing) to meet the linear model assumptions of homoscedasticity and residuals normality. We included all the variables in a global model per response variable and then selected the best model using the package MuMIn (Bartoń, 2023), which is based on Akaike information criteria (AICc). When models were considered equally good ($\Delta \text{AICc} < 2$), we averaged these models. We performed a Tukey test when appropriate for canopy strata, and performed an ANOVA test for each model to test the overall effect of each factor. All the analyses were carried out with R software (R Core Team, 2024).

3. Results

For species richness, there was an interaction between restoration method and canopy strata (Table 1). The top stratum in eucalypt plantations was dominated by eucalypt trees, which decreased in dominance in the upper-middle stratum and were not present in the lower ones (Fig. 2-b, d). The abundance of native species followed the opposite trend: low in the top stratum and highest in the lower ones (Fig. 2-b, d). The mean maximum stratum height of naturally regenerating forests and mature forests were lower than in eucalypt plantations (Fig. 2-c, f, i). Forest strata had a similar species richness both in the naturally regenerating forests and in the mature forests (Fig. 2-e, h), with all the strata mostly composed of native species (Fig. 2-g, j).

The average linear mixed models indicate that functional composition is mainly determined by canopy strata and its interaction with restoration method, and CWD (Table 2). Restoration method (eucalypt plantation with natural regeneration or naturally regenerating forest) was included in all models but it was significant only for CWM SLA and bark thickness (Table 2). Naturally regenerating forests had lower values for bark thickness, and higher values for SLA than eucalypt plantations (Table 2). Canopy strata were significant in all models, and their interaction with restoration method was significant for all traits except for leaf thickness (Table 2, Fig. 3). CWM wood density for both eucalypt plantations with regeneration and naturally regenerating forests was lower in the lower stratum (Fig. 3-a). Bark thickness increased from the lower to top stratum, but bark thickness of the top stratum was significantly higher in eucalypt plantations than in naturally regenerating forests (Fig. 3-b). In eucalypt plantations, the CWM SLA decreased from the lower to the top stratum, whereas in naturally regenerating forests SLA did not differ among strata (Fig. 3-c). The top stratum from eucalypt plantations had a lower proportion of N-fixing trees compared to all other strata (Fig. 3-d), whereas naturally regenerating forests had a

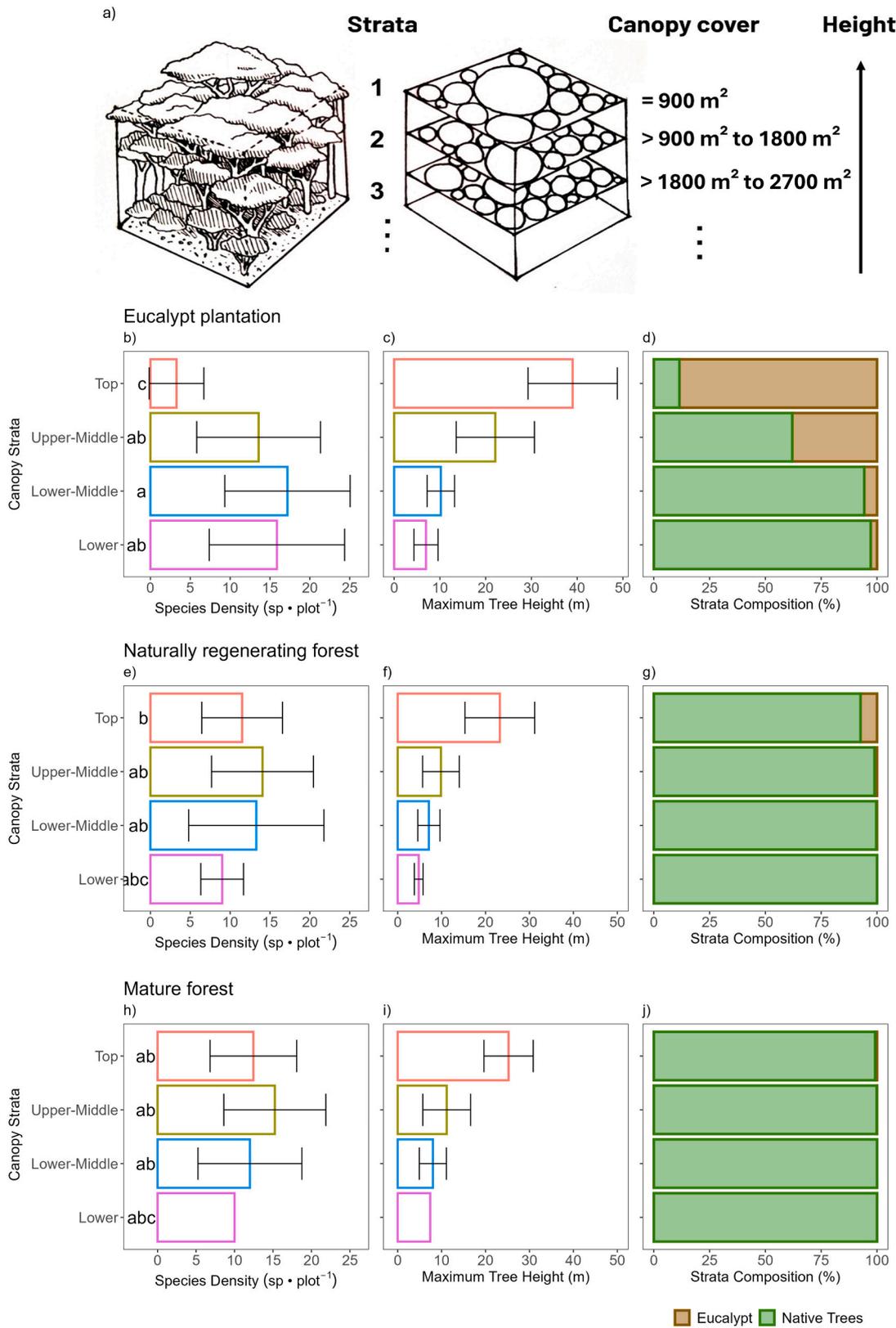


Fig. 2. Canopy strata assignment method scheme (a). The method consists of ordering the trees found in a 900 m² plot from the tallest to the shortest tree and summing up their crown area until the cumulative crown area reaches the plot area, assigning these trees to the top stratum. This procedure is repeated until all trees in the inventory are assigned to a canopy stratum. (b) to (j) describe characteristics of the canopy strata in eucalypt plantations with natural regeneration (b, c, d), naturally regenerating forests (e, f, g), and mature forests (h, i, j). Species richness (b, e, h) is the mean species number (\pm SD) per stratum per plot. Different letters mean the strata are statistically different in terms of species richness. Maximum height (c, f, i) is the mean height (\pm SD) of the tallest tree per stratum per plot. The proportion of strata composition (d, g, j) is the total proportion of each stratum, composed of eucalypt trees or native trees. Illustration: Ari F. de Toledo Jr.

Table 1

ANOVA results for species richness (species per plot). Statistical significance: “**” = $p \leq 0.05$, “****” = $p \leq 0.001$.

Factors	df	F-value
Restoration method	2	3.91*
Canopy strata	3	14.27***
Restoration method x Canopy strata	6	8.4***
Residuals	337	

similar proportion of N-fixing trees in all strata.

CWD had a significant effect on all traits but N-fixation (Table 2). Drier sites had higher CWM wood density and SLA, but lower bark and leaf thickness. Plot age had a significant effect on three traits: older stands had higher CWM wood density and bark thickness, and a larger proportion of N-fixing trees. Interaction between canopy strata and plot age for CWM wood density (Table 2, Suppl. Mat. S3: Figs. S3–1)

The landscape variable, terrain slope, had a marginal negative influence on CWM leaf thickness. Soil characteristics had little effect on functional composition; plots on soils with higher clay content had reduced bark thickness, soil pH positively influenced proportion of N-fixing trees, while SB was not included in any of the models.

4. Discussion

We assessed whether functional composition differs between naturally regenerating forests and eucalypt plantations with native tree species regeneration underneath their canopy. Functional composition was strongly determined by canopy strata, often in interaction with restoration method (eucalypt plantation with natural regeneration or naturally regenerating forest) and CWD, whereas stand age, and soil characteristics had, surprisingly, little effect.

4.1. Eucalypt trees influence the functional composition of the tree community, mostly in the top canopy stratum

Eucalypt plantations with natural regeneration had denser wood and thicker bark than naturally regenerating forests, mainly because of planted eucalypt trees that occupied the top stratum (Table 2, Fig. 2-b,d) whereas in naturally regenerating forest the top stratum is dominated by soft-wooded fast-growing pioneer species. Dense wood allows eucalypts to attain taller maximal tree size, and to be more resistant to drought-induced cavitation because high wood density is associated with smaller pit pores and structural enforcement against implosion of cavitated vessels (Hacke et al., 2001, 2023). A thick bark protects eucalypt trees against fire, although high litter production and biomass accumulation make eucalypt plantations more flammable (White et al., 2014; Santos et al., 2019), which can be detrimental for native species regenerating in their understory.

The middle strata of eucalypt plantations with natural regeneration had few to no regenerating eucalypt trees, and had similar functional properties as the naturally regenerating forest. Surprisingly, in both forests the lowest stratum had lower wood density than the other strata (Fig. 3-a) probably because most plots that had a lower stratum and two thirds of the lower stratum trees were located in wet or moist areas, which tend to have a lower wood density (Poorter et al., 2019b).

Eucalypts are drought adapted by having dense leaves with low SLA (Steane et al., 2017), whereas they cannot fix N. As eucalypts dominate the upper two strata of the plantations, these strata had lower CWM SLA and a lower proportion of N fixers than the two lower strata (Fig. 3-c). We expected that the marked increase in light availability from the understory to the canopy, light acclimation, and differences in shade tolerance between understory species and canopy species would have opposite consequences for community SLA in different strata. On the one hand, within species, plants acclimate to an increase in light by making thicker leaves with more palisade parenchyma layers, resulting in higher

Table 2
Averaged linear mixed models for the assessed community-weighted means (CWM) traits and F-test for all included variables. We included the estimates only for binary and continuous variables. TYPE = restoration method, STR = canopy strata, AGE = stand age, CWD = climatic water deficit, SLOPE = terrain slope, CLAY = soil clay content, pH = soil pH, SLA = specific leaf area, df1 = numerator degree of freedom, df2 = denominator degree of freedom. Restoration method is a categorical variable with two levels: naturally regenerating forest and eucalypt plantation with natural regeneration. Canopy strata is a categorical variable with four levels: top stratum, upper-middle stratum, lower-middle stratum, and lower stratum. The differences in the relationship among strata are detailed in Fig. 3. Statistical significance: ‘.’ = $p \leq 0.1$, ‘*’ = $p \leq 0.05$, ‘***’ = $p \leq 0.01$, ‘****’ = $p \leq 0.001$.

	TYPE	STR	TYPE X STRATA	log (AGE)	log (AGE) X STR	CWD	SLOPE	CLAY	pH	R ²
log (Wood density)	Estimate	-0.46		0.17		0.25				0.57
	F-value	1.27		26.55	7.30	10.32				
	df1	1	3	1	3	1				
log (Bark thickness)	df2	151.66	5.47	217.74	162.78	96.53				0.73
	Estimate	-1.14	155.55	0.12		-0.39		-0.15		
	F-value	5.46	***	14.90	4.15	29.94	***	4.85	*	
SLA	df1	1	3	1	1	1		1		
	df2	108.84	136.27	88.20		77.70		77.42		0.68
	Estimate	1.64				0.31				
log (Leaf thickness)	F-value	33.69	***			30.55	***			
	df1	1	3			1				
	df2	143.37	167.03			98.86				0.64
log (N-fixing)	Estimate	-0.21				-0.52			-0.07	
	F-value	2.12	***			31.06	***		0.78	
	df1	1	3			1			1	
log (N-fixing)	df2	87.17				90.76			92.11	
	Estimate	1.17	***	11.18					0.20	0.67
	F-value	3.22	***	4.14	*				5.61	
log (N-fixing)	df1	1	3	1		1			1	
	df2	123.37	148.61	98.41					90.29	

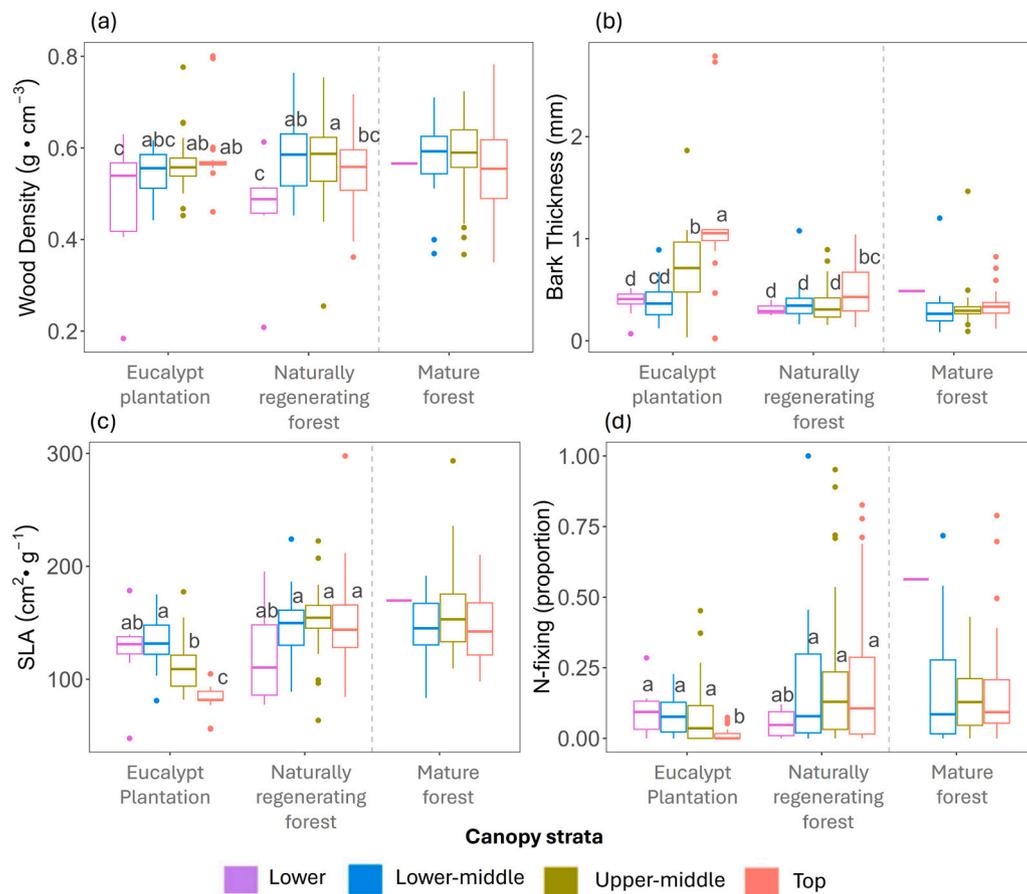


Fig. 3. Interaction effect of restoration method and canopy strata on the CWM (Community Weighted Mean) of four functional traits. N-fixing is given as a categorical variable (1 = N-fixer, 0 = not N-fixer). Different letters mean the strata are statistically different. Mature forests were not included in the analyses but are provided as a reference.

photosynthesis per unit leaf area and lower SLA (Poorter et al., 2019a). This would result in lower SLA in higher strata. On the other hand, shade tolerant species that tend to occupy the lower forest strata, produce long lived leaves with low SLA, whereas light demanding pioneer species that occupy the upper strata, produce short lived leaves with high SLA. This would result in higher SLA in higher strata (Rozenaal et al., 2006; Liu et al., 2010). Yet, both in eucalypt plantations and naturally regenerating forests we found no differences among the strata that were mainly composed of native species. Possibly, the canopy of these forests is more permeable to light than expected, especially in the eucalypt canopy where the vertical hanging leaves intercept less light, thus mitigating the influence of the canopy position on the CWM SLA. Similarly, the strata that were mostly composed of native species, did not differ in the proportion of nitrogen fixing trees.

Our results strongly suggest that, although the presence of eucalypt trees changes the overall functional composition of the tree community, they do not strongly influence the functional composition of regenerating native tree species under the canopy, since most of the differences between the plantations and naturally regenerating forests were found in the top stratum (Fig. 3). These results indicate that if eucalypt trees growing in plantations with natural regeneration are harvested, the CWM of some traits of the leftover native vegetation will be similar to those of naturally regenerating forests. In fact, when we removed eucalypt trees from the analyses, restoration method and the interaction between restoration method and canopy strata was not significant for bark thickness, SLA, and N-fixing (Suppl. Mat. S3: Table S3-1). However, since eucalypt trees are planted in a high density, there is a trade-off between wood supply and environmental outcomes (Naime et al., 2020; Hua et al., 2022). Another interesting aspect is that the CWM

values in naturally regenerating forests do not differ much from mature forests, which indicates that, in terms of functional composition, the naturally regenerating forests are recovering towards the mature forest values. This result is consistent with Poorter et al., (2021a), who also observed a fast functional recovery in naturally regenerating forests. Furthermore, Brouwer et al. (2025), who also presented results from the same studied plots, observed that tree monocultures with natural regeneration can recover towards mature forests values, even though they take a much longer time than restoration plantings or naturally regenerating forests. The differences found between the functional composition in eucalypt plantations with natural regeneration and naturally regenerating forests are driven by the presence of eucalypt trees rather than by the native tree species functional composition. This result implies that when eucalypt plantations are less intensively managed, they can contribute to forest restoration by fostering native tree regeneration with a similar functional composition than naturally regenerating forests, while also potentially providing financial benefits to landowners if and when they opt to harvest the eucalypt trees.

4.2. Climatic water deficit plays an important role in functional composition

Climatic water availability, represented by CWD, was relevant for all assessed traits except for the proportion of N-fixing trees (Table 2). Drier areas with high absolute CWD had higher wood density, SLA, and thinner leaves and bark. In line with our hypothesis, community assembly in drier sites followed a conservative strategy regarding wood density and acquisitive strategies regarding community leaf traits (SLA and leaf thickness). The early successional tree community in drier sites

tend to present higher wood density to avoid stem damage induced by drought, while in wet sites, the trees invest less in wood density to prioritize fast growth since water limitation is not an issue (Poorter et al., 2021b). Climate variables are more relevant than soil fertility for SLA values (Liu et al., 2017), with drier sites generally having deciduous species that prioritize leaf productivity, low production costs and protection against water loss instead of longevity; therefore, producing thinner leaves and with higher SLA (Lohbeck et al., 2013; Matsuo et al., 2024b). On the other hand, in sites where water availability is high, plants are able to invest in thicker and long-lasting leaves.

We expected CWM bark thickness to be higher in drier areas since they are more susceptible to fire events and the bark protects them (Hoffmann et al., 2003). However, we found that drier areas had thinner bark, probably because bark thickness tends to increase with stem diameter (Poorter et al., 2014) and our dry sites were less productive and had, on average, thinner trees.

The lack of substantial influence of the soil characteristics, important component for determining local water availability, might be a reflex of the soil sampling depth. For practical reasons, we collected only a superficial layer, which may not be sufficient to completely understand the soil dynamics and its effects on vegetation, since trees root system that can explore deeper soil layers for water uptake, especially in dry periods (Burgess et al., 1998; Bleby et al., 2010). Climatic water availability, in this case, was more important for determining functional composition, having an imperative role in determining the resource-use strategy of the colonizing plants, regardless of the restoration method. Our results support that understanding plant resource-use strategies that are adequate for each environment and climate is key for selecting appropriate species for successful restoration efforts.

4.3. Forest strata, more than successional age, determine functional composition

Time since intensive management practices were interrupted (after agriculture or active plantation management) only significantly increased the proportion of N-fixing trees and CWM wood density and CWM bark thickness (Table 2). Most studies found that the proportion of N-fixing species decreased over time (Batterman et al., 2013; Gei et al., 2018; Taylor et al., 2019), probably because a successional decline in light availability does not allow plants to sustain the high energetic costs needed to support symbiotic nitrogen fixing bacteria. The contrasting pattern observed in our study may be attributed to the distribution of our plots across different vegetation types. Specifically, 55 % of our younger plots (less than 40 years old) are located in humid, evergreen rainforests, whereas only 17 % of the older plots are situated in this vegetation type. Dry forests, such as seasonal and transitional forest-savanna ecosystems, tend to have a higher relative abundance of nitrogen-fixing (N-fixing) trees, and although the relative abundance of N-fixing trees declines with forest age, it remains higher in dry forests compared to rainforests (Gei et al., 2018). This uneven distribution of evergreen and seasonal forest plots across age classes led to an increase in the overall proportion of N-fixing trees in the study as function of age. Furthermore, 41 % of the variance in N-fixing was explained by the random plot effect in our study. Other studies also found considerable site-to-site variation (Menge and Chazdon, 2016; Gei et al., 2018), indicating that site-specific conditions can influence the colonization and establishment of N-fixers within a forest stand (Gei et al., 2018).

CWM wood density increased with stand age, indicating a replacement of soft-wooded fast-growing pioneers by slow-growing, persistent shade-tolerant species. We did not observe the expected opposite successional pathways, with dry forests proceeding from high to low CWM wood density values during succession and wet forests from low to high CWM wood density values (Poorter et al., 2019b), since the interaction between age and CWD was not significant. Bark thickness was positively related to stand age. While bark thickness varies among tree species, variation within species is tree size is mainly attributed to tree size

(Paine et al., 2010), which explains higher CWM bark thickness values in older stands.

The fact that we did not find an effect of age on all studied traits is surprising since time is an important factor for forest succession (Meiners et al., 2015; Poorter et al., 2024; van Breugel et al., 2024). Most likely, this age effect is captured by the number of canopy strata that increase with succession from one layer to four layers (Matsuo et al., 2021; Rüger et al., 2023). Canopy strata, often in interaction with restoration method, had a significant effect on all traits (Table 2), being more important to determine functional composition than the stand age in this study. These results have important implications for forest restoration, since they suggest that the community traits recover toward values found in mature forests over time, even with the presence of eucalypt trees.

4.4. Implications for forest landscape restoration

The two restoration methods differed in their community trait values, which indicates that the functions provided by the restored forest will also be different and, in the case of eucalypt plantations, strongly influenced by the presence of eucalypt trees. While eucalypt plantations with natural regeneration have higher climate mitigation potential because eucalypt trees grow faster than native trees, these plantations are also more susceptible to fires, and nutrient cycling might be slower than in naturally regenerating forests. Therefore, the chosen restoration method will depend on the objectives of the stakeholders, and which functions they want to prioritize. If wood production is not the main goal, other restoration methods can be more adequate than eucalypt plantations (Hua et al., 2022).

Mixed plantations of eucalypts and native species have been proposed as a way to improve landscape connectivity or as an intermediate step in forest restoration, helping to offset its costs (Brancalion et al., 2020). Although the community's functional composition, shaped by the presence of eucalypt trees, differs between the two restoration methods included in this study, eucalypts did not strongly influence the functional composition of the regenerating native species growing in the two lower strata of the forests (Fig. 3). These results show the potential of these plantations to allow natural regeneration when management practices such as weeding and understorey clearing are discontinued or plantations are abandoned after harvesting.

Young naturally regenerating forests are repeatedly cut as part of a shifting cultivation system, for conversion to agricultural use or other reasons in Brazil (Piffer et al., 2022) and other in tropical countries (Reid et al., 2019). In contrast, for timber plantations, there are clear financial incentives for maintaining saw wood production over decades, which results in better environmental outcomes than a young, naturally regenerating forest that is repeatedly cut. Eucalypt plantations that are managed less intensively with longer rotation periods may have, therefore, the potential to deliver both ecological and economic benefits and work as a valuable lever to increase the area and longevity of reforestation sites in dynamic, human-modified landscapes.

CRediT authorship contribution statement

Mathieu Decuyper: Writing – review & editing, Methodology. **José G. Fernandes Neto:** Writing – review & editing, Data curation. **Almeida Danilo R. A.:** Methodology, Data curation. **Miguel Cooper:** Writing – review & editing, Resources, Methodology. **Juliano van Melis:** Writing – review & editing, Data curation. **Joannès Guillemot:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology. **Paulo G. Molin:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Matheus S. Fuza:** Visualization, Formal analysis. **Simões Laura H. P.:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lima Renato A. F.:** Writing – review &

editing, Data curation. **Marielos Peña-Claros:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lourens Poorter:** Writing – review & editing, Visualization, Methodology, Funding acquisition. **Catherine T. de Almeida:** Writing – review & editing, Methodology, Data curation. **Rens Brouwer:** Writing – review & editing, Project administration, Methodology, Formal analysis, Data curation. **Frans Bongers:** Writing – review & editing, Visualization, Project administration, Methodology, Funding acquisition. **Vinicius C. Souza:** Investigation, Data curation. **Ari F. de Toledo:** Visualization. **Angélica F. Resende:** Writing – review & editing, Methodology, Data curation. **Ricardo R. Rodrigues:** Writing – review & editing, Methodology, Funding acquisition. **Toledo Cássio A. P.:** Investigation, Data curation. **Brancelion Pedro H. S.:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

PHS Brancelion and RR Rodrigues are partners at Re.green, a restoration company. DRA Almeida is partner at Biofore, a restoration monitoring company.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122952](https://doi.org/10.1016/j.foreco.2025.122952).

Data availability

Data will be made available on request.

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